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Maximum swimming speed predictions for *Mullus barbatus* (Linnaeus, 1758) and *Diplodus annularis* (Linnaeus, 1758)

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Abstract: Maximum swimming speed of red mullet (*Mullus barbatus*) and annular sea bream (*Diplodus annularis*) was estimated based on muscle twitch experiments. The maximum estimated speed of red mullet (mean length: 16.9 cm) was 3.14 m/s (18.6 bl/s) at 26 °C. At 20 °C the maximum estimated speed of annular sea bream (mean length: 11.5 cm) was 1.92 m/s (16.7 bl/s). Maximum swimming speed of annular sea bream decreased as the temperature decreased.

Key words: Red mullet, annular sea bream, maximum speed, muscle contraction, temperature

Mullus barbatus (Linnaeus, 1758) ve *Diplodus annularis* (Linnaeus, 1758) için maksimum yüzme hızı tahminleri

Özet: Barbun (*Mullus barbatus*) ve isparoz (*Diplodus annularis*) balıklarının maksimum yüzme hızları hesaplanmıştır. Ortalama vücut boyu 16,9 cm olan bir barbunun 26 °C de maksimum yüzme hızının saniyede 3,14 m (18,6 vücut boyu) olduğu tahmin edilmiştir. Ortalama vücut boyu 11,5 cm olan bir isparozun 20 °C de maksimum yüzme hızının saniyede 1,92 m (16,7 vücut boyu) olduğu tahmin edilmiştir. Bu tür için ayrıca maksimum yüzme hızının azalan sıcaklıkla düştüğü gözlenmiştir.

Anahtar sözcükler: Barbun, isparoz, maksimum hız, kas kasılımı, sıcaklık

Introduction

Swimming performance is the main characteristic that determines survival in many species of fish and other aquatic animals (Plaut, 2001). There are 3 levels of swimming activity (Özbilgin et al., 2004) and several methodologies for measuring swimming performance. Sustained (as endurance), prolonged (as critical swimming speed), and burst (as maximum) swimming ability are commonly used measures of performance in fish (Hammer, 1995).

The speed of a steadily swimming fish is the product of stride length and tail beat frequency (Wardle, 1975). One fish stride is the distance moved forward after 1 complete left-right cycle of the tail at

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a steady swimming speed. Each species is thought to have a maximum stride length, and when swimming steadily a fish simply modifies its speed by adjusting its tail beat frequency (Videler, 1993). To achieve maximum swimming speed, therefore, fish must use the best possible stride length with the highest possible tail beat frequency.

Wardle (1975) was the first researcher to predict the maximum tail beat frequency of fish based on muscle contraction experiments. He suggested that fish need to contract the myotomes on each side of the body consecutively to perform a tail beat; therefore, the minimum time required to complete 1 tail beat could not be shorter than twice the minimum contraction time of the swimming muscles on 1 side of the body. He measured the contraction time of muscle blocks dissected from freshly killed fish by stimulating them with a single electric pulse (20 V for 1 ms) in a temperature-controlled saline solution. He also recorded the movements of fast swimming fish with a modified closed circuit television system by racing or startling them. The predictions he made based on muscle contraction experiments were similar to the observed tail beat frequency of the species, which he managed to record at fast swimming speeds. Wardle (1975) concluded that the muscle contraction time of a fish limited the maximum attainable tail beat frequency and, thus, the maximum swimming speed.

It is generally recognized that the body temperature of all fish, except some large scombrids (Brill et al., 1994) and large sharks (Bone and Marshall, 1982), is closely related to the water temperature, even when they are working very hard (Özbilgin, 2002). Water temperature varies in time and space, and has a profound impact on almost all aspects of fish physiology (Wooton, 1992), including swimming performance (He, 1993; Videler, 1993; Wardle and He, 1996; Özbilgin, 2002; Özbilgin and Wardle, 2002; Özbilgin and Başaran, 2005).

Wardle (1975, 1977, 1980) reported that the contraction time of the white muscle of fish increased as the water temperature increased. He also reported that for fish of equal length the minimum contraction time was similar when measured under the same environmental conditions, irrespective of species; the larger the fish, the longer the muscle contraction time, resulting in lower maximum tail beat frequency. These conclusions were subsequently supported by Arimoto et al. (1991), who observed an increase in muscle contraction from 60 to 80 ms for fish 20-30 cm long (walleye pollock, *Theregra chalcogramma*) and from to 90 to 120 ms for fish 40-50 cm long at a water temperature of 2 °C.

The literature contains a limited quantity of data on swimming performance in fishes in the Mediterranean Sea. Only a few of the studies that investigated the subject (e.g. Koumoundouros et al., 2002; Başaran et al., 2007a, 2007b; Özbilgin and Başaran, 2005) used critical swimming speed methodology, which is an easy means of measuring swimming performance and involves having fish swim at incrementally higher speed until exhaustion (Plaut, 2001). The present study aimed to predict the maximum swimming speed of 2 commercially exploited fish species based on stride length measurement and minimum muscle contraction time. The effect of fish length on muscle contraction time in red mullet (*Mullus barbatus*), and the effect of muscle temperature change on contraction time in annular sea bream (*Diplodus annularis*) were investigated under laboratory conditions.

Materials and methods

All the experiments were conducted at Ege University, Fisheries Faculty, Urla-İskele Fish Behavior Laboratory during August and September 2005. Video recordings of steadily swimming red mullet and annular sea bream in a current channel were used to measure stride length. Detailed descriptions and technical drawings of the swimming channel are provided by Özbilgin and Başaran (2005), and Başaran et al. (2007a, 2007b). The time for 3 tail beats at a fixed water velocity was measured, and the time to complete 1 tail beat was calculated for each observation. Ten observations for each species were analyzed and mean values were computed. The distance traveled with 1 tail beat was calculated and stride length was calculated as the ratio of that distance to the length of the fish.

Muscle contraction experiments were conducted with 12 red mullet (mean length: 16.9 ± 0.63 cm) and 11 annular sea bream (mean length: 11.5 ± 0.28 cm).

The fish were captured during demersal trawling operations in İzmir Bay. All the fish rested for at least 2 days prior to the experiments. Fishes used for stride length measurement and the twitch experiment were from the same group; however, to avoid undue stress they were not necessarily the same individuals.

An instrument was designed to measure muscle contraction speed (Figure 1), which included 5 main components:

-Electric stimulator;

-Power unit;

-Recording unit;

-Temperature control unit;

-Recording box.

Figure 1. Instrument used for measuring muscle contraction speed.

The fish were measured (total length), killed, and a block representing the anterior dorsal white lateral muscles was removed from just behind the dorsal part of the gills, as in Özbilgin (2002), and Özbilgin and Wardle (2002). Muscle samples were placed on 2 needle electrodes of a metal plate of a piezoelectric force transducer (Figure 2). A single pulse electric stimulus of ~20 mA was applied to the muscle block for 1 ms via the 2 needles. The electric pulse stimulated a single muscle contraction known as a twitch. The time from the start of the electric pulse stimulus to the peak (maximum force) of the contraction was calculated using computer software specific for this purpose. Contractions were stimulated in 5% dextrose lactate solution in the recording box; the temperature of the muscle block was altered by heating or cooling this solution.

Figure 2. Fish muscle sample placed on needle electrodes of the measuring box.

For red mullet 10 measurements were obtained at 26 °C for each fish at 5-s intervals. For annular sea bream the temperature was reduced from 20 to 10 °C and 1 measurement was obtained at 0.3-°C intervals.

Results

Mean muscle contraction time in the 12 red mullets was 15.8 ms (SE 0.59) at 26 °C. Tail beat frequency was 1000/(15.8 × 2) = 32 Hz. Stride length was estimated as 0.58 body length (bl). A red mullet 16.9 cm long can reach a maximum speed of 3.14 m/s or 18.6 bl/s at a muscle temperature of 26 °C. While the absolute maximum speed (as m/s) tended to increase as fish length increased (Figure 3 and Table), the relative maximum speed (as bl/s) tended to decrease (Table).

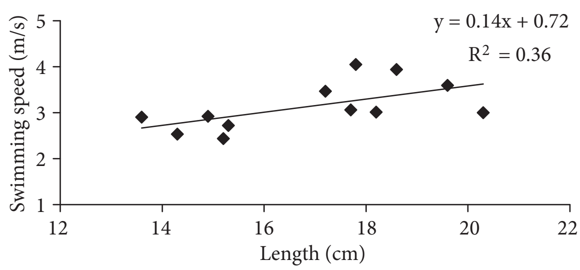

Figure 3. Length burst speed relationship of red mullet at 26 °C.

Table. Maximum swimming speed estimations of 12 red mullet at 26 °C.

Length (cm)	Mean contraction time (ms)	Tail beat frequency (Hz)	Predicted Maximum swimming speed* (bl/s)	Predicted Maximum swimming speed* (m/s)
20.3	19.62 ± 0.16	25.5	14.8	3.00
14.3	16.38 ± 0.27	30.5	17.7	2.53
13.6	13.59 ± 0.13	36.8	21.3	2.90
15.2	18.10 ± 0.10	27.6	16.0	2.44
17.2	14.39 ± 0.09	34.8	20.2	3.47
18.2	17.53 ± 0.06	28.5	16.5	3.01
17.7	16.77 ± 0.07	29.8	17.3	3.06
18.6	13.70 ± 0.09	36.5	21.2	3.94
19.6	15.82 ± 0.64	31.6	18.3	3.59
17.8	12.75 ± 0.23	39.2	22.7	4.05
15.3	16.29 ± 0.07	30.7	17.8	2.72
14.9	14.81 ± 0.08	33.8	19.6	2.92

* For maximum speed predictions, mean stride length value of 0.58 body length was used.

Muscle contraction time in the annular sea bream decreased logarithmically as temperature increased from 10 and 20 °C. The relationship between temperature and contraction time was generally described well with logarithmic regression lines for the individual fish data (Figure 4); however, the combined data for 11 fish produced a relatively scattered fit (Figure 5), which is indicative of the variation in their maximum swimming performance. Muscle contraction time, calculated with the logarithmic regression equation of the combined data, for 10, 15, and 20 °C was 22.1, 19.9, and 18.3 ms, respectively. Estimated tail beat frequency based on these values was 22.6 Hz for 10 °C, 25.1 Hz for 15 °C, and 27.3 Hz for 20 °C. Stride length was estimated as 0.61 body length. For annular sea bream (mean length: 11.5 cm) maximum speed at 10 °C was 1.58 m/s or 13.8 bl/s, at 15 °C it was 1.76 m/s or 15.3 bl/s, and at 20 °C it was 1.92 m/s or 16.7 bl/s.

Discussion and conclusion

The present study is the first to obtain data on the estimated maximum swimming speed of red mullet and annular sea bream; therefore, direct comparison of the results with those of other studies is not possible. Nonetheless, both size- and temperature-related critical speed changes in annular sea bream were previously reported by Özbilgin and Başaran (2005), which are in agreement with the present results for maximum speed predictions.

Maximum swimming performance in annular sea bream was temperature dependent; it was significantly lower at a water temperature of 10 °C than at 20 °C in all of the experimental animals. Muscle contraction time decreased logarithmically as temperature increased. In other words, the effect of a 1-degree temperature change on muscle contraction time decreased as the temperature increased. Physiological effects of temperature change are generally described as $Q_{10\,°C}$ effects, where $Q_{10\,°C}$ is the increase in the rate caused by an increase in temperature of 10 °C (Videler, 1993). If a rate doubles over a temperature increase of 10 °C, $Q_{10\,°C}$ is 2 and if it triples $Q_{10\,°C}$ is 3. If R_1 and R_2 are the tail beat frequencies at 2 temperatures (t_1 and t_2),

$$R_2 = R_1 \, . \, Q_{10\,°C}^{\,(t_2 - t_1)/10}$$

$Q_{10\,°C}$ can be calculated from the following equation:

$$Q_{10\,°C} = (R_2/R_1)^{\,10/(t_2 - t_1)}$$

If we assume that the shortest time to complete a tail beat is limited by the muscle twitch contraction time, we can calculate the $Q_{10\,°C}$ for the group of annular sea bream 10.1-13.9 cm long in a temperature range of 10-20 °C. The mean tail beat frequency in these fish, calculated from the logarithmic regression equations of muscle twitch time and temperature (Figure 5), was 22.6 Hz at 10 °C and 27.3 Hz at 20 °C. This gives a $Q_{10\,°C}$ value of 1.21. For sand flathead

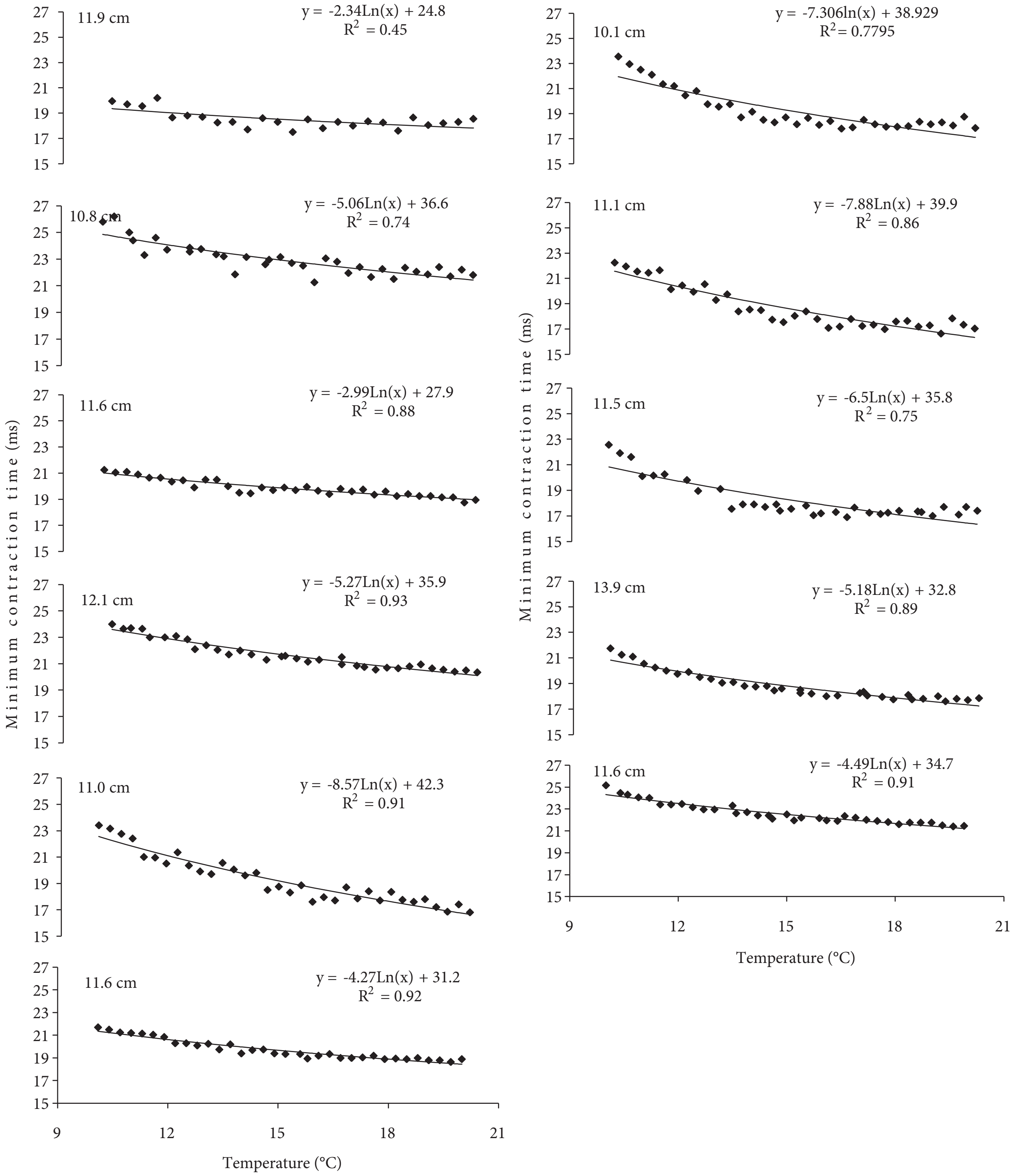

Figure 4. Annular sea bream. Individual fish data and logarithmic regression lines.

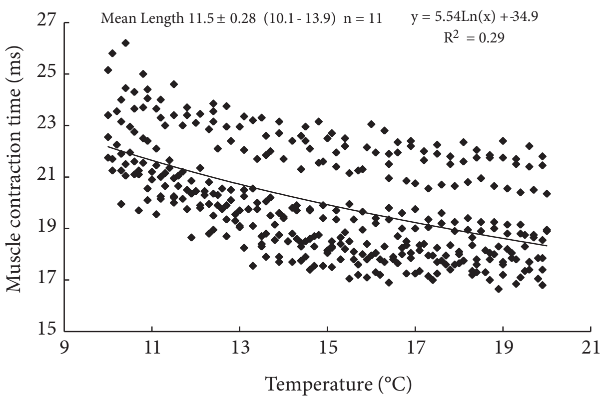

Figure 5. Annular sea bream. Combined fish data and logarithmic regression line.

(*Platycephalus bassensis*) Yanase et al. (2007) reported $Q_{10\,°C}$ values of 1.83 and 1.28 between 10 and 15 °C, and between 15 and 20 °C, respectively. Videler and Wardle (1991) calculated $Q_{10\,°C}$ values for cod (*Gadus morhua*) at 7 temperatures between 2 and 15 °C and reported a mean value of 2.06. The $Q_{10\,°C}$ value calculated in the present study is much lower than that reported for cod, which was obtained at lower temperatures, and is more similar to the value for sand flathead, which was determined in the same temperature range, yet is lower than the expected value, as a $Q_{10°C}$ value of about 2 is common for the rate of speed of biological enzyme-catalyzed chemical reactions (Videler and Wardle, 1991; Videler, 1993).

Wardle (1975, 1980), Arimoto et al. (1991), and Yanase et al. (2007) reported an increase in muscle contraction time as fish length increased. A similar scale effect was observed in red mullet; muscle contraction time tended to increase in larger fish. Analogous to the Q_{10} for temperature, a Q_{10} value for the effect of size differences can be defined. Q_{10cm} is the ratio of the maximum tail beat frequency for each 10-cm change in length (Videler and Wardle, 1991). Özbilgin (1998) studied muscle twitch in 2 haddock size groups (mean lengths 30 and 41 cm) and calculated Q_{10cm} values of 0.96 at 7 °C and 0.88 at 12 °C. Videler and Wardle (1991) reported a mean Q_{10cm} value of 0.89 for 8 sizes of cod (from 20 to 84.5 cm) at 7 temperatures between 2 and 15 °C. In the present study the Q_{10cm} value, estimated from the linear regression line fitted to the muscle contraction time of all experimental red mullet (length range between 13.6 and 20.3 cm), was 0.95. This value is in line with those reported in the above-mentioned studies.

The maximum stride length of a fish represents its top gear and usually varies between 0.5 and 1 bl (Videler and Wardle, 1991). Özbilgin (1998) reported a stride length of 0.734 bl for haddock and 0.728 bl for whiting (*Merlangius merlangus*). In the present study stride length was 0.58 for red mullet and 0.61 for annular sea bream. These values were obtained during steady swimming at intermediate speeds, and they are not necessarily the highest values these species can achieve; therefore, the maximum values could be even higher than that predicted in the present study if the fish use greater stride lengths. Such examples were reported for several species by Videler and Wardle (1991), and Yanese et al. (2007) for sand flathead. Wardle and He (1988) reported a stride length of 1 bl for a 31-cm mackerel (*Scomber scombrus*) swimming at 18 bl/s (tail beat frequency of 18 Hz) in water of 12 °C, based on measurements obtained with a high-speed camera. The muscle twitch contraction time they measured at the same temperature for mackerel of the same size was 0.026 s, which predicted a maximum tail beat frequency of 19 Hz.

Although the fastest burst swimming is of very short duration (Wardle, 1980), it is of great survival value to fish during escape (He, 1993); therefore, it is necessary to understand how fast a fish can swim and what its ecological relevance is. For example, all estimated maximum swimming speeds obtained in the present study are in excess of the typical commercial trawl towing speed of 1.5 m/s. However, fish usually avoid use of this behavior unless it is a matter of survival (Wardle, 1993). Any burst-swimming activity in a trawl codend is unlikely to be at maximum speed due to previously accumulated fatigue, and will be even less during the winter months (Yanase et al., 2007). Muscle contraction data are useful for predicting how fast a fish can swim. Nevertheless, to better understand the escape behavior of fish, such data need to be supported by both high-speed camera observations in the laboratory and, if possible, underwater observations at sea. Data on the escape behavior of commercially exploited fishes in the Mediterranean Sea are rather limited and deserve further study.

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